A cortical and cerebellar parcellation system for speech studies

Jason Tourville and Frank Guenther

November, 2003

Technical Report CAS/CNS-2003-022

Boston University Center for Adaptive Systems
and
Department of Cognitive and Neural Systems
677 Beacon Street
Boston, MA 02215

A Cortical and Cerebellar Parcellation System for Speech Studies

Jason A. Tourville[1] & Frank H. Guenther[1,2,3]

[1]Department of Cognitive and Neural Systems, Boston University, 677 Beacon St, Boston, MA 02215
[2]Research Laboratory of Electronics, Massachusetts Institute of Technology, Cambridge, MA
[3]Department of Radiology, Massachusetts General Hospital, Charlestown, MA

Keywords: speech, cortex, parcellation, functional imaging

Boston University Technical Report CAS/CNS-TR-03-022

Abstract

A neuroanatomical parcellation system is described which encompasses the entire cerebral cortex and the cerebellum. The cortical system is a modified version of the scheme described by Caviness et al. (1996) and is designed particularly for studies of speech processing. The cerebellum is parcellated into 6 cortical regions of interest (ROIs) and an ROI representing the deep cerebellar nuclei in each hemisphere. The boundaries of each ROI are based on individual anatomical markers that are clearly visible from standard structural MRI acquisitions. The system permits averaging of functional imaging data sets from multiple subjects while accounting for individual anatomical variability. Used in conjunction with region-of-interest analysis techniques such as that described by Nieto-Castanon et al. (2003), the parcellation system provides a more powerful means of analyzing functional data.

1 INTRODUCTION

To obtain a fine-grained functional map of the cortical interactions underlying speech, it is first necessary to parcellate the speech-related areas of cortex into smaller functional units. Traditionally defined speech-related cortical areas, such as "Wernicke's area", "Broca's area", and "auditory cortex", involve large expanses of cortex and are often inconsistently used in the literature. For example, portions of the supramarginal gyrus, angular gyrus, and/or middle temporal gyrus are sometimes included in the definition of Wernicke's area (Penfield and Roberts, 1959), while other researchers limit Wernicke's area to the posterior superior temporal gyrus and planum temporale (Martin, 1996; Kuehn, Lemme, and Baumgartner, 1989). Similarly, Broca's area is sometimes limited to Brodmann's Area (BA) 44 (Martin, 1996), while other definitions also include BA 45 (Duvernoy, 1999; Goodglass, 1993). Even more confusing, the term auditory cortex is sometimes used to refer only to primary auditory cortex (BA 41) and other times to primary and higher-order auditory cortical areas (BA 42, 22, and 52), prompting the neuroanatomist Duvernoy (1999, p. 46) to note that "the precise localization of the auditory cortex seems difficult to define

A finer-grained parcellation scheme based on anatomical landmarks has been created for the purpose of analyzing the volumes of different regions of cortex (Caviness et al., 1996). This system, developed and used extensively at the Center for Morphometric Analysis (CMA) at Massachusetts General Hospital, has allowed researchers to compare brains of neurologically normal subject populations to brains of individuals with psychiatric disorders such as schizophrenia in an attempt to identify the brain regions involved in these disorders. Many of the anatomical landmarks defining borders between different parcellation units, or regions of interest (ROIs), align approximately with cytoarchitectonic maps of cortex (e.g., the well-known Brodmann areas). It is commonly assumed that cytoarchitecture and normal function of a brain region are closely related, as evidenced by the use of functional names for many of Brodmann's areas; e.g. BA 4 is commonly called primary motor cortex and BA 41 is commonly called primary auditory cortex in the neuroscience literature. The CMA parcellation scheme of can thus be thought of as a means to identify functional brain regions using anatomical landmarks that are clearly visible on structural MRI images (unlike cytoarchitectonic details, which are impossible to identify in standard structural MRI scans).

Because the Caviness et al. parcellation scheme was not specifically designed for the study of speech and speech disorders, it is not ideally suited for our speech neuroimaging studies. In particular, several of the ROIs in the CMA system are not defined at a fine-enough grain for detailed study of the sensory and motor bases of speech. We therefore created a modified version of the Caviness et al. parcellation scheme that is specifically geared to speech studies. Following a review of relevant physiological and imaging studies of speech processing, a set of speech-related cortical ROIs was defined. To assess the functional role of cortical regions not typically associated with speech processing, ROIs representing the remainder of the cerebral cortex were also defined and largely follow the conventions of the CMA system. In addition to modifying the CMA cerebral cortex parcellation system, a set of ROIs within the cerebellum was defined based upon the anatomical atlas of Schmahmann et al. (2000).

2 CORTICAL/CEREBELLAR PARCELLATION SYSTEM

Speech-related cortical ROIs

Table 1 provides a list of speech-related cortical regions and possible functional contributions to speech processing for each. The table also lists approximate Brodmann area correlates for each of the regions of interest, when applicable. Based on the results of a number of recent neuroimaging studies of speech (see Table 1), a modified version of the Caviness et al. cortical parcellation system was created for the purpose of functionally mapping cortical interactions involved in speech processing. The new scheme is illustrated in Figure 1. The following significant changes were made to the Caviness et al. system:

Superior Temporal Sulcus: The dorsal and ventral banks of the superior temporal sulcus are defined separately from the surrounding temporal lobe gyri (superior and middle, respectively). This change reflects imaging studies that suggest a phoneme processing center within the superior temporal sulcus (Binder et al., 2000; Scott et al., 2000; Belin et al., 2000; Wise et al., 2001). Cutting planes orthogonal to the cortical surface are made at the lateral margins of the dorsal and ventral surfaces of the superior temporal sulcus to delineate cortex lying within the sulcus from the gyral cortex lying on the exposed surface. A third cutting plane is made through the fundus of the superior temporal sulcus to divide the dorsal and ventral surfaces of the sulcus. The boundary separating anterior and posterior temporal lateral temporal lobe ROIs (superior, middle, and inferior temporal gyrus, and dorsal and ventral superior temporal sulcus) remains the anterior extent of Heshl's gyrus.

Heshl's Gyrus: To obtain a consistent, reliable definition of Heshl's gyrus, the guidelines for defining this area described by Kim et al. (2000) have been adopted. Their method addresses the difficulty encountered when multiple transverse gyri are present along the superior temporal plane. Heshl's gyrus is typically defined as lying between the first transverse fissure and Heshl's sulcus. A "double Heshl's" arises when a transverse fissure lies lateral to Heshl's sulcus, creating two "bumps" on the superior temporal plance. In the event of a "double Heshl's", if Heshl's sulcus extends caudomedially behind the insula, then it serves as the lateral border along the entire extent Heshl's gyrus. If Heshl's sulcus terminates anterior to the posterior end of the insula, then it serves as the lateral border of Heshl's gyrus caudomedially to the point of its termination. Posterior to this point, Heshl's gyrus extends laterally to the more lateral transverse fissure. This method provides a reliable method for defining primary auditory cortex that reflects architectonic studies of this area (e.g. Rivier & Clarke, 1997; Wallace et al., 2002).

Posterior Extension of the Superior Temporal Gyrus: The posterior portion of the superior temporal gyrus extends posteriorly to the intermediate fissure of Jensen. As a result, the posterior portion of supramarginal gyrus borders superior temporal gyrus ventrally, rather than extending further ventrally to the superior temporal sulcus, as it does in the Caviness et al. system. This modification better reflects the boundary between BA 40 and BA 22.

Insular Region: The insula is divided into anterior and posterior regions along the central insular sulcus. This change is motivated by studies that suggest a role in articulatory planning within the anterior insula (e.g., Dronkers, 1996).

Motor Cortices: The precentral gyrus contains both primary motor and premotor cortices. Therefore, we divide the gyrus into anterior (premotor) and posterior (motor) regions. Since the ventral portion of the precentral gyrus is devoted to the speech articulators, we also divide the premotor and motor regions into ventral and dorsal subregions. On the medial surface, anterior to the precentral sulcus, the supplementary motor area (SMA) is divided into anterior and posterior regions based on recent results that suggest separate functional roles for these two regions (e.g., Boecker et al.,1998). The rostro-caudal level of the anterior commissure serves to divide the two SMA regions. The anterior region extends rostrally to the level of the interior portion of the genu of the corpus callosum, based on the parcellation system of Crespo-Faccoro et al. (2000). Immediately lateral to the two SMA regions, on the dorsal surface, two additional

Region (ROIs)	BA	Possible Function
Heschl's gyrus (Hg)	41	Center frequency/frequency sweep encoding (Shreiner, 1995; Wang & Shamma, 1995); Sound level encoding (Brechmann et al., 2002)
Insula (aINS, pINS)	--	Articulatory planning (anterior; Dronkers, 1996; Wise et al., 1999; Kuriki et al., 1999)
Middle Temporal gyrus (aMTg, pMTg)	21	Lexical/semantic processing (Indefrey & Levelt, 2000)
Motor Cortex and anterior Central Operculum (dMC, vMC,aCO)	4,43	Primary motor cortex for speech articulators (Penfield & Roberts, 1959)
Planum Polare (PP)	52	Syntactic processing (Friederici et al., 2000)
Planum Temporale (PT)	42	Complex tone processing (Mummery et al. 1999); CV syllable perception (Jäncke et al., 2002)
Inferior Frontal gyrus and Frontal Operculum (IFt, IFo, FO)	44,45	Semantic processing (Giraud & Price, 2001); Grapheme-to-phoneme conversion (Newman & Twieg, 2001)
Dorsal Premotor Cortex (adPMC, mdPMC, pdPMC)	6	Initiation and sequential planning of speech movements (Jonas, 1987)
Ventral Premotor Cortex (vPMC)	6	Planning of speech utterances at acoustic and articulatory levels
Somatosensory Cortex and posterior Central Operculum (vSC,pCO)	1,2,3,43	Primary somatosensory cortex for speech articulators (Penfield & Roberts, 1959)
Superior Temporal gyrus (aSTg, pSTg)	22	Anterior: processing of speech-like sounds (Binder et al, 2000, Scott et al, 2000). Posterior: phonological processing for speech perception and production (Hickok & Poeppel, 2000; Buchsbaum et al., 2001)
Superior Temporal sulcus (adSTs, avSTs, pdSTs, pvSTs)	22	Anterior: phoneme processing; (Binder et al., 2000; Scott et al., 2000; Belin et al., 2000). Posterior: perception/retrieval of single words (Wise et al., 2001)
Supplementary Motor Area (aSMA, pSMA)	6	Motor sequencing (Wildgruber et al., 1999); Initiation of articulation (Ziegler et al. 1997); Articulatory planning (Indefrey & Levelt, 2000)
Supramarginal gyrus and Parietal Operculum (aSMg, pSMg, PO)	40	Phonological processing for speech perception (Caplan et al., 1995; Celsis et al, 1999) and production (Geschwind, 1965; Damasio & Damasio, 1980); Sound localization of speech source (Weeks et al., 2000; Rauschecker & Tian, 2000)

Table 1: Brodmann areas (BA) and possible function of brain regions in our parcellation scheme. **Parcellation unit key: CO**=central operculum; **FO**=frontal operculum; **IFo**=inferior frontal gyrus, pars opercularis; **IFt**=inferior frontal gyrus, pars triangularis; **Hg**=Heschl's gyrus; **aINS**=anterior insula; **pINS**=posterior insula; **dMC**=dorsal primary motor cortex; **vMC**=ventral primary motor cortex; **aMTg**=anterior middle temporal gyrus; **pMTg**=posterior middle temporal gyrus; **adPMC**=anterior dorsal premotor cortex; **mdPMC**=middle dorsal premotor cortex; **pdPMC**=posterior dorsal premotor cortex; **PO**=parietal operculum; **PP**=planum polare; **PT**=planum temporale; **aSMA**=anterior supplementary motor area; **pSMA**=posterior supplementary motor area; **aSMg**=anterior supramarginal gyrus; **pSMg**=posterior supramarginal gyrus; **vSC**=ventral somatosensory cortex; **aSTg**=anterior superior temporal gyrus; **pSTg**=posterior superior temporal gyrus; **adSTs**=anterior dorsal superior temporal sulcus; **avSTs**=anterior ventral superior temporal sulcus; **pdSTs**=posterior dorsal superior temporal sulcus; **pvSTs**=posterior ventral superior temporal sulcus.

premotor regions are defined. They extend laterally to the superior frontal sulcus and share the same boundary markers as the adjacent SMA regions.

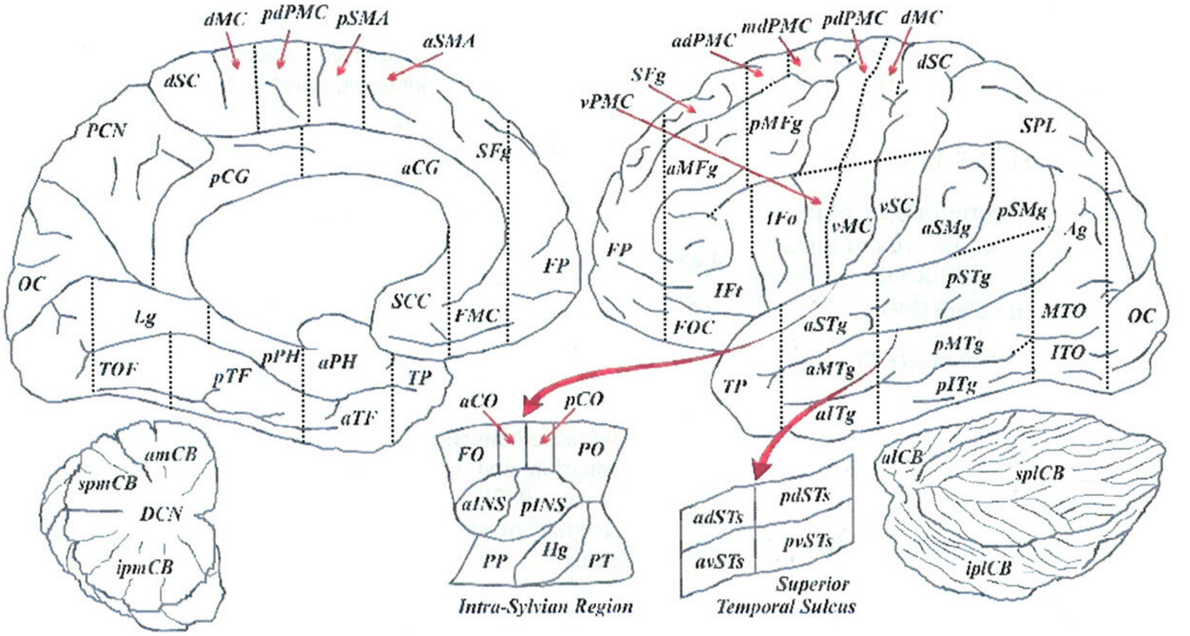

Figure 1: A cortical and cerebellar parcellation scheme based on Caviness et al. (1996) and Schmahmann et al (2000) parcellation systems . Speech-related cortical regions of interest (ROIs) are highlighted in gray on the lateral (right) and medial (left) brain surfaces of the left hemisphere. Dashed lines indicated boundaries between adjacent regions. The Intra-Sylvian region and the Superior Temporal sulcus are schematized as exposed flattened surfaces as indicated by the two sweeping red arrows. The detached labeled cerebellum is also shown in the lower left and lower right. See Table 1 for abbreviation definitions of the speech-related ROIs, Table 2 for remaining cortical ROIs and Table 3 for cerebellar ROIs.

Somatosensory Cortex: The portion of the postcentral gyrus lateral to the intraparietal sulcus is labeled ventral somatosensory cortex. This region receives sensory information from the speech articulators (Penfield & Roberts, 1959).

Remaining cortical ROIs

Recent functional imaging work has demonstrated the involvement of a wide expanse of the cerebral cortex in speech processing. It is therefore useful to anatomically characterize the entire cerebral cortex, not simply the core speech-related areas described above. To assess activity in the remainder of the cerebral cortex, we have largely adopted the CMA. system. A few minor modifications were made to accommodate the changes to the speech-related regions described above. When necessary, the nomenclature was also made consistent with that used to describe the speech-related ROIs. For example, the post-central gyrus, labeled POG by Caviness et al., is now split into two ROIs, ventral and dorsal somatosensory cortex (vSC, dSC). Table 2 provides a list of the remaining cortical ROIs along with their approximate correspondence with the parcellation units of Caviness et al. and Brodmann areas. The schematic in Figure 1 shows the location of these ROIs on the cortical surface.

The principal areas of modification lie at the rostral and caudal ends of the brain. Rostrally, the paracingulate gyrus has been eliminated. The superior frontal gyrus (SFg), frontal pole (FP), and frontal medial cortex (FMC) extend ventrally, caudally, and dorsally, respectively, to the cingulate sulcus. This change allows for a more reliable parcellation of frontomedial cortex as it eliminates reliance upon the paracingulate sulcus, which is typically highly segmented and often difficult to locate. In the event of a "double cingulate" (see Ono et al, 1990), the outer cingulate sulcus serves as the rostrodorsal border of the cingulate gyrus. Also on the frontal lobe, SFg (termed F1 in CMA system) has been truncated posteriorly to allow for the presence of the dorsal premotor ROIs (adPMC and mdPMC) laterally and the anterior supplementary motor area (aSMA) medially.

Caudally, regions of the occipital lobe of been lumped in to one ROI, the occipital cortex (OC). As in the CMA system, the occipital lobe is bordered anteriorly by the parietooccipital fissure medially and the point of opercularization of the intraparietal sulcus laterally (Plane F). However, all cortex behind these boundaries is now collapsed into a single ROI. In addition to eliminating a number of occipital ROIs, the posterior border of lingual gyrus (LG) is moved anteriorly to Plane F. These changes allow for the elimination of a number of boundary planes in the CMA system that are difficult to define (in particular the rostral and caudal ends of the cuneal sulcus) without sacrificing anatomical specificity that is relevant to speech research.

Cortical ROIs	Caviness et al. Label	Brodmann Areas
Angular Gyrus (Ag)	AG	39
Cingulate Gyrus (aCG, pCG)	CGa, CGp, PAC	23, 24, 29, 30, 33
Dorsal Somatosensory Cortex (dSC)	POG	1, 2, 3, 5
Frontal Medial Cortex (FMC)	FMC	11, 12, 32
Frontal Orbital Cortex (FOC)	FOC	11, 13, 14, 47
Frontal Pole (FP)	FP, PAC	9, 10, 12
Inferior Temporal Gyrus (aITg, pITg)	T3a, T3p	20, 37
Inferior Temporal Occipital Gyrus (ITO)	TO3	37, 19
Lingual Gyrus (Lg)	LG	18, 19, 37
Middle Frontal Gyrus (aMFg, pMFg)	F2	8, 9, 46
Middle Temporal Occipital Gyrus (MTO)	TO2	19, 37
Occipital Cortex (OC)	OP, OLs, OLi, OF, LG, CALC, SCAL, CN	17, 18, 19
Parahippocampal Gyrus (aPH, pPH)	PHa, PHp	27, 28, 34, 35, 51
Precuneus Cortex (PCN)	PCN	7a, 7b, 23, 31
Subcallosal Cortex (SCC)	SC	12, 15, 24, 25, 32, 33
Superior Frontal Gyrus (SFg)	F1, PAC	8, 9
Superior Parietal Lobule (SPL)	SPL	7a, 7b
Temporal Fusiform Gyrus (aTF, pTF)	TFa, TFp	20, 36, 37
Temporal Occipital Fusiform Gyrus (TOF)	TOF	19, 37
Temporal Pole (TP)	TP	38

Table 2: ROIs covering the remainder of the cerebral cortex are listed along with approximate Caviness et al. (1996) and Brodmann area correspondence. Several of the regions listed consist of anterior and posterior segments. Note that a single ROI may consist of cortex represented by several Caviness and/or Brodmann areas. In these cases, all the areas contributing to the ROI are listed. Conversely, a single Caviness and/or Brodmann area may represent cortex in multiple ROIs.

Cerebellar ROIs

The cerebellum has been shown to play a role both in both speech production and speech perception (e.g., Ackermann et al., 1999; De Nil et al., 2000; Wildgruber et al., 2001; Mathiak et al., 2002). To better localize cerebellum involvement in speech related tasks, we have adopted a simplified version of the cerebellum parcellation system described by Schmahmann et al (2000). The cortex of each cerebellar hemisphere is split into six ROIs, three medial and lateral pairs (see Figure 2, top). Dividing medial from lateral regions is the sagittal plane that falls one third of the way between the midline and the lateral extent of each hemisphere, termed Plane Cb. The primary and horizontal fissures, along with the hemispheric margins provide the remainder boundaries for the cortical ROIs. Thus, the anatomical markers that define region boundaries are easily identified. The anterior medial and anterior lateral ROIs (amCB, alCB) lie anterior to the primary fissure. Behind this fissure, superior and inferior regions are divided by the horizontal fissure. The superior posterior medial and lateral ROIs (spmCB, splCB) lie dorsal to the horizontal fissure while the inferior posterior medial and lateral (ipmCB, iplCB) lie ventral to it.

Finally, we define a deep cerebellar nuclei (DCN) ROI. The difficulty associated with localizing the deep cerebellar nuclei on MRI slices necessitates a gross definition relative to the other ROIs described here. The nuclei lie medially within cerebellar white matter (the area completely enclosed by the cortical ribbon after the cortex has been segmented). The goal of the region definition is to eliminate as much of this area as possible that is not DCN without discarding any portion of the nuclei. Thus, the DCN ROI is an overestimate of the nuclei. Only the dentate nucleus is readily viewable on standard MRI data sets and lateral extent of this

	Boundaries			
Cerebellar ROIs	**Anterior**	**Posterior**	**Medial**	**Lateral**
Anterior Lateral (alCB)	Anterior H.M.	Primary Fissure	Plane Cb	Lateral H.M.
Anterior Medial (amCB)	Anterior H.M.	Primary Fissure	Midline	Plane Cb
Inferior Posterior Lateral (iplCB)	Posterior H.M.	Posterior H.M.	Plane Cb	Horizontal Fissure
Inferior Posterior Medial (ipmCB)	Posterior H.M.	Posterior H.M.	Midline	Plane Cb
Superior Posterior Lateral (splCB)	Primary Fissure	Posterior H.M.	Plane Cb	Horizontal Fissure
Superior Posterior Medial (spmCB)	Primary Fissure	Posterior H.M.	Midline	Plane Cb
Deep Cerebellar Nuclei (DCN)*	Brainstem, Posterior End	alCB, Posterior End	Midline	Dentate Nuc., Lateral Border

Table 3: Cerebellar ROIs listed with their anatomical boundaries. Plane Cb is a sagittal plane one third of the way between the midline of the cerebellum and its lateral extent. H.M. = hemispheric margin.
* Because the deep cerebellar nuclei are difficult to view on standard structural data sets acquired on 15T or 3T magnets, these boundaries serve as easily identified gross approximations of the extents of the deep cerebellar The nuclei, provided brains are in Talairach space (oriented along the anterior commissure – posterior commisure line). DCN ROI lies entirely within the region of the cerebellum that is enclosed by the cerebellar cortical ribbon, therefore this entire region could serve as an alternative ROI definition.

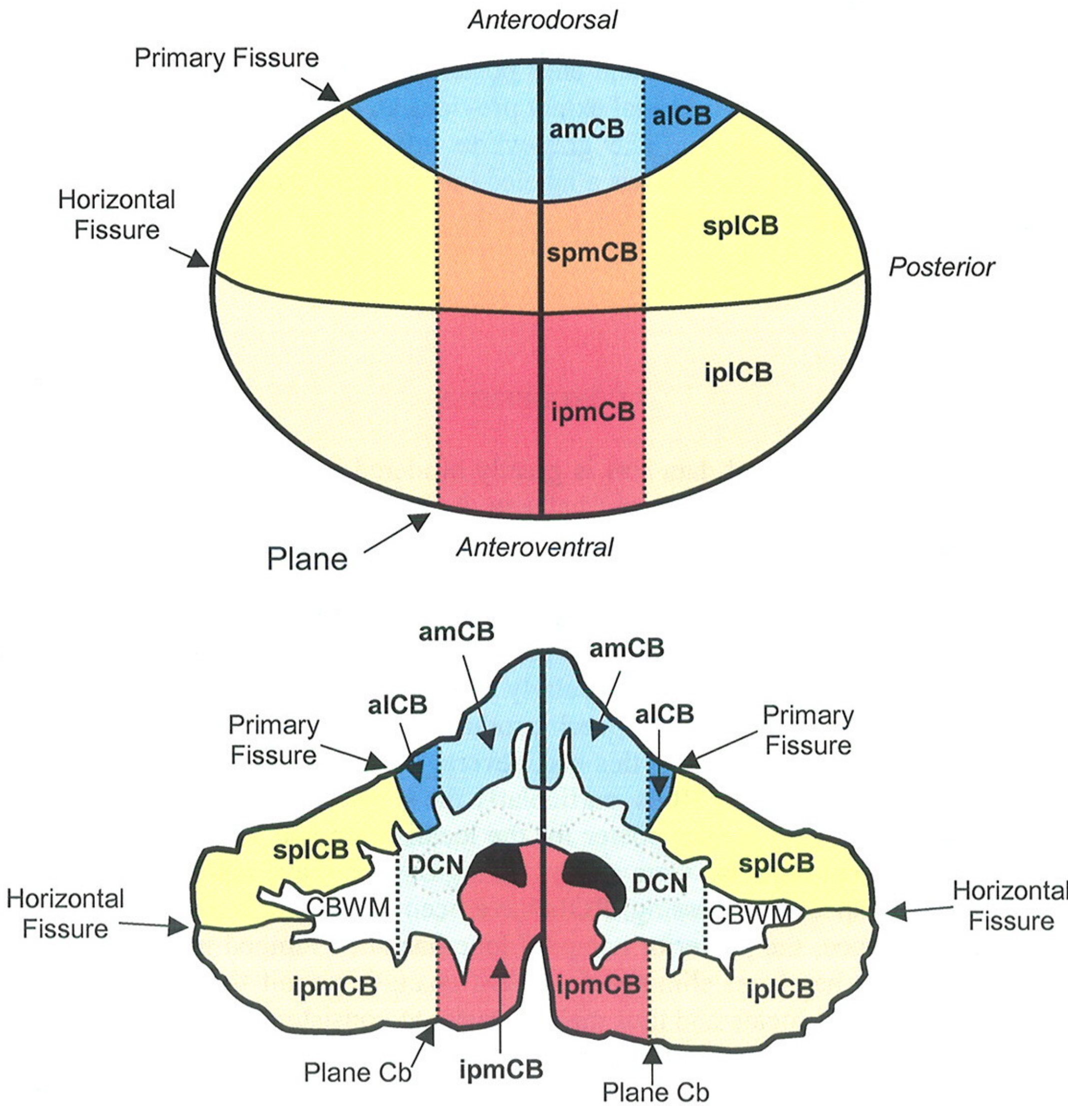

Figure 2: Parcellation of the cerebellum. Top: Labeled ROIs on a schematized flattened cerebellar cortical surface. The top of the figure corresponds to the anterior extent of the dorsal surface of the cerebellum and the bottom corresponds to the anterior extent of the ventral surface. Plane Cb marks the plane one third of the way between the cerebellum midline and the lateral margin. The primary and horizontal fissures serve as the other boundary markers. Bottom: Labeled coronal slice. The cerebellum ROIs are shown on a representative coronal slice. The DCN ROI can be seen within the cerebellum white matter (CBWM). The light gray dotted lines represents an approximate outline the deep cerebellar nuclei within the DCN ROI. See the text for a description of the boundaries of DCN. Refer to Table 3 for an explanation of ROI abbreviations.

nucleus serves as a rough lateral boundary for DCN. The anterior and posterior DCN borders are grossly defined using extrinsic anatomical markers. DCN begins anteriorly on the posterior-most coronal slice containing brainstem and ends posteriorly on the posterior-most slice coronal slice containing amCB. This rostro-caudal extent provides an overestimate of the range of slices containing deep cerebellar nuclei. The gray-white interface forms the dorsal and ventral boundaries. The bottom of Figure 2 shows a labeled coronal slice through the cerebellum. Both the cortical and DCN ROIs can be seen.

3 CONCLUSIONS

The analysis of functional data sets is greatly hindered by the high degree of individual anatomical variability across brains (Nieto-Castanon et al., 2003). To ensure comparison of like brain areas, regions of interest must be defined according individual anatomical markers prior to averaging. Here we have described a parcellation system that encompasses the entire cerebral cortex and the cerebellum based on individual anatomical markers that are discernable from standard MRI data sets. Based largely on the parcellation scheme described by Caviness et al. (1996), the system was designed to be particularly well suited for studies of speech processing. Cortical areas shown to be involved in speech production and/or perception were redefined to reflect know functional boundaries. To this end, several of the Caviness et al. parcellation units were subdivided into more discrete ROIs, particularly the superior temporal sulcus and premotor areas. These changes provide greater power for the localization and functional characterization of speech-relevant cortical regions. Conversely, for regions that have not been shown, as yet, to play a specific role in speech processing, ROIs have been combined to allow for more reliable parcellation. For instance, the posterior occipital lobe has been lumped into a single ROI, and the paracingulate gyrus has been eliminated. These changes permit the removal of boundary markers that are difficult to locate and thus make it easier to consistently define regions.

The parcellation system described here is meant to serve as a starting point. Several of the regions, even those known to play a role in speech processing, such as the cerebellar ROIs, are crudely defined. This was done either in the interest of definition reliability or because there is insufficient information to support more strictly defined regions. Advances in imaging techniques will likely lead to greater ease in localizing boundary markers. The potential for greater advances, however, lies in well-designed functional studies of speech processing that target specific brain regions. For instance, we have recently begun studies that utilize stimulus parameterizations that will allow us to localize topographic maps along the superior temporal plane. The goal of this research is to further subdivide this core auditory area into more functionally relevant regions. Other studies are searching for specific sites within the cerebellum and premotor regions that contribute to speech production. Thus, the parcellation scheme will be continually updated according to the results of speech-related research.

REFERENCES

Ackermann H., Graber S., Hertrich I., Daum I. (1999). Phonemic vowel length contrasts in cerebellar disorders. *Brain Lang.* 67(2):95-109.

Belin, P., Zatorre, R.J., Lafaille, P., Ahad, P., and Pike, B. (2000). Voice-selective areas in human auditory cortex. *Nature,* **403,** pp. 309-312.

Binder, J.R., Frost, J.A., Hammeke, T.A., Bellgowan, P.S., Springer, J.A., Kaufman, J.N., and Possing, E.T. (2000). Human temporal lobe activation by speech and nonspeech sounds. *Cerebral Cortex,* **10**, pp. 512-528.

Boecker, H., Dagher, A., Ceballos-Baumann, A.O., Passingham, R.E., Samuel, M., Friston, K.J., Poline, J., Dettmers, C., Conrad, B., and Brooks, D.J. (1998). Role of the human rostral supplementary motor area and the basal ganglia in motor sequence control: investigations with H2 15O PET. *Journal of Neurophysiology,* **79**, pp. 1070-1080.

Brechmann, A., Baumgart, F., and Scheich, H. (2002). Sound-level-dependent representation of frequency modulations in human auditory cortex: a low-noise fMRI study. *Journal of Neurophysiology,* **87**, pp. 423-33.

Buchsbaum, B.R., Hickok, G., and Humpries, C. (2001). Role of left posterior superior temporal gyrus in phonological processing for speech perception and production. *Cognitive Science,* **25**, pp. 663-678.

Caplan, D., Gow, D., Makris, N. (1995). Analysis of lesions by MRI in stroke patients with acoustic-phonetic processing deficits. *Neurology,* **45**, pp. 293-298.

Caviness, V.S., Meyer, J., Makris, N., Kennedy, D.N. (1996). MRI-based topographic parcellation of human neocortex: an anatomically specified method with estimate of reliability. *Journal of Cognitive Neuroscience,* **8**, pp. 566-587.

Celsis, P., Boulanouar, K., Doyon, B., Ranjeva, J.P., Berry, I., Nespoulous, J.L., Chollet, F. (1999). Differential fMRI responses in the left posterior superior temporal gyrus and left supramarginal gyrus to habituation and change detection in syllables and tones. *Neuroimage,* **9**, pp. 135-144.

Crespo-Facorro, B., Kim, J., Andreason, N.C., Spinks, R., O'Leary, D.S., Bockholt, H.J., Harris, G., Magnotta, V. (2000). Cerebral cortex: a topographic segmentation method using magnetic resonance imaging. *Psychiatry Research: Neuroimaging Section,* **100**, pp. 97-126.

Damasio, H., and Damasio, A.R. (1980). The anatomical basis of conduction aphasia. *Brain,* **103**, pp. 337-350.

De Nil L.F., Kroll R.M., Houle S. (2001). Functional neuroimaging of cerebellar activation during single word reading and verb generation in stuttering and nonstuttering adults. *Neurosci Lett.* 302(2-3):77-80.

Dronkers N.F. (1996). A new brain region for coordinating speech articulation. *Nature,* **384**, pp. 159-161.

Duvernoy, H.M. (1999). *The human brain: Surface, blood supply, and three-dimensional anatomy* (2nd edition). New York: Springer-Verlag Wien.

Friederici, A.D., Meyer, M., and von Cramon, D.Y. (2000). Auditory language comprehension: an event-related fMRI study on the processing of syntactic and lexical information. *Brain and Language*, **75**, pp. 289-300.

Geshwind, N. (1965). Disconnexion syndromes in animals and man. I. *Brain,* **88**, pp. 237-294.

Giraud, A.I. and Price, C.J. (2001). The constraints functional neuroimaging places on classical models of auditory word processing. *Journal of Cognitive Neuroscience*, **13**, pp. 754-65.

Goodglass, H. (1993). *Understanding aphasia.* New York: Academic Press.

Hickok, G., and Poeppel, D. (2000). Towards a functional neuroanatomy of speech perception. *Trends in Cognitive Sciences,* **4**, pp. 131-138.

Indefrey, P. and Levelt, W.J.M. (2000). The neural correlates of language production. In M. Gazzaniga (Ed.), *The New Cognitive Neurosciences* - 2nd Edition (pp. 845-865). Cambridge, MA: MIT Press.

Jäncke, L., Wustenberg, T., Scheich, H., Heinze, H.J. (2002). Phonetic perception and the temporal cortex. *Neuroimage*, **15**, pp. 733-46.

Jonas, S. (1987). The supplementary motor region and speech. In E. Perecman (Ed.), *The Frontal Lobes Revisited* (pp. 241-250). New York: IRBN Press.

Kim J.J., Crespo-Facorro B., Andreasen N.C., O'Leary D.S., Magnotta V., Nopoulos P. (2000). Morphology of the lateral superior temporal gyrus in neuroleptic naive patients with schizophrenia: relationship to symptoms. *Neuroimage.* 11:271-288.

Kuehn, D.P., Lemme, M.L., and Baumgartner, J.M. (1989). *Neural bases of speech, hearing, and language.* Austin, Texas: Pro-ed.

Kuriki, S., Mori, T., Hirata, Y. (1999). Motor planning center for speech articulation in the normal human brain. *Neuroreport,* **10,** pp. 765-769.

Martin, J.H. (1996). *Neuroanatomy: Text and atlas* (2nd edition). Stamford, CT: Appleton & Lange.

Mathiak K., Hertrich I., Grodd W., Ackermann H. (2002). Cerebellum and speech perception: a functional magnetic resonance imaging study. *J Cogn Neurosci.* 14(6):902-12.

Mummery, C.J., Ashburner, J., Scott, S.K., Wise, R.J. (1999). Functional neuroimaging of speech perception in six normal and two aphasic subjects. *Journal of the Acoustical Society of America,* **106**, pp. 449-57.

Newman, S.D. and Tweig, D. (2001). Difference in auditory processing of words and pseudowords: An fMRI study. *Human Brain Mapping,* **14**, pp. 39-47.

Nieto-Castanon, A., Ghosh, S.S., Tourville, J.A., and Guenther, F.H. (2003). Region-of-interest based analysis of functional imaging data. *NeuroImage,* 19:1303-1316.

Ono, M., Kubik, S., Abernathy, C.D. (1990). *Atlas of the Cerebral Sulci.* Stuttgart: Georg Thieme Verlag.

Penfield, W., and Roberts, L. (1959) *Speech and brain mechanisms.* Princeton, NJ: Princeton University Press.

Rauschecker, J.P., Tian, B. (2000). Mechanisms and streams for processing of "what" and "where" in auditory cortex. *Proceedings of the National Academy of Sciences*, **97**, pp. 11800-11806.

Rivier F., Clarke S.. (1997). Cytochrome oxidase, acetylcholinesterase, and NADPH-diaphorase staining in human supratemporal and insular cortex: evidence for multiple auditory areas. *Neuroimage.* 6:288-304.

Schreiner, C.E. (1995). Order and disorder in auditory cortical maps. *Curr Opin Neurobiol* **5**(4), pp. 489-96.

Schmahmann J.D., Doyon J., Toga A.W., Petrides M., Evans A.C. (2000). *MRI Atlas of the Human Cerebellum*. San Diego: Academci Press.

Scott, S.K., Blank, C.C., Rosen, S., Wise, R.J. (2000). Identification of a pathway for intelligible speech in the left temporal lobe. *Brain,* **123**, pp. 2400-2406.

Wallace MN, Johnston PW, Palmer AR. (2002). Histochemical identification of cortical areas in the auditory region of the human brain. *Exp Brain Res.* 143:499-508.

Wang, K. and Shamm, S.A. (1995). Spectral shape analysis in the central auditory system. *IEEE Trans. on Speech and Audio Processing,* **3**, pp. 382-395.

Weeks, R.A., Aziz-Sultan, A., Bushara, K.O., Tian, B., Wessinger, C.M., Dang, N., Rauschecker, J.P., and Hallett, M. (1999). A PET study of human auditory spatial processing. *Neuroscience Letters*, **262**, pp. 155-158.

Wildgruber D., Ackermann H., Grodd W. (2001). Differential contributions of motor cortex, basal ganglia, and cerebellum to speech motor control: effects of syllable repetition rate evaluated by fMRI. *Neuroimage.* 13(1):101-9.

Wildgruber, D., Kischka, U., Ackermann, H., Klose, U., Grodd, W. (1999). Dynamic pattern of brain activation during sequencing of word strings evaluated by fMRI. *Cognitive Brain Research,* **7**, pp. 285-294.

Wise, R.J., Greene, J., Buchel, C., Scott, S.K. (1999). Brain regions involved in articulation. *Lancet,* **353**, pp. 1057-1061.

Wise, R.J., Scott, S.K., Blank, S.C., Mummery, C.J., Murphy, K., Warburton, E.A. (2001). Separate neural subsystems within 'Wernicke's area.' *Brain,* **124**, pp. 83-95.

Ziegler, W., Kilian, B., Deger, K. (1997). The role of the left mesial frontal cortex in fluent speech: evidence from a case of left supplementary motor area hemorrhage. *Neuropsychologica*, **35**, pp. 1197-1208.